

In Situ Measurement of Radular Movements of Three Species of *Littorina* (Gastropoda: Littorinidae)

by

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Abstract. Radular movements of the periwinkle species *Littorina littorea*, *L. obtusata*, and *L. saxatilis* were measured *in situ* by an underwater microphone. The rates of activity are similar in all three species and are between 28 and 42 rasps/min. The rate of radular activity of *L. littorea* is reduced in larger animals, in animals from the lower intertidal zone, and on surfaces encrusted with *Semibalanus balanoides*. The greatest decline in radular activity is 30% and occurs on irregular surfaces such as those of *S. balanoides*.

INTRODUCTION

ON ROCKY intertidal shores of New England, periwinkles (*Littorina littorea* Linnaeus, *L. obtusata* Linnaeus, *L. saxatilis* Olivi) are the most abundant of the herbivorous gastropods. Impact of periwinkle grazing activity is greater on smooth surfaces (LUBCHENCO, 1983), in protected sites (LUBCHENCO & MENGE, 1978), in tidal pool (LUBCHENCO, 1978, 1982), and on lower intertidal shores (LUBCHENCO & MENGE, 1978; LUBCHENCO, 1983). Yet, periwinkles feed only when submerged or moistened (NEWELL, 1958a, b; Petraitis, personal observations), and NEWELL *et al.* (1971), by timing rasps per minute for 15-30 sec on the sides of aquaria, showed that *L. littorea* from the upper shore have a higher rate of radular activity than those from the lower shore. NEWELL *et al.* (1971) suggested that differences in rates reflected a compensation for differences in the amount of time spent submerged, so that the per individual impact was the same regardless of intertidal position. Thus, it is not clear whether longer duration of submersion or higher densities of snails accounts for their greater impact in tidal pools and on lower intertidal shores. Furthermore, on irregular surfaces, such as in crevices and among barnacles, better success of perennial algae may be due not only to ineffective grazing by periwinkles but also to higher recruitment of algae and lower mortality of germlings as a result of physical factors such as reduced desiccation of germlings in crevices.

Therefore, it was of interest to measure directly the rate of radular activity of *Littorina littorea*, *L. obtusata* and *L. saxatilis* in the field using techniques developed by KITTING (1979).

MATERIALS AND METHODS

All observations and experiments were done at two locations on Swan's Island in Hancock County, Maine, U.S.A. Most of the work was done on Long Cove (44°8'10"N, 68°26'15"W). A south-facing shore, this site is a very protected, nonestuarine, cobble beach with occasional granite outcrops. *Semibalanus balanoides* (Linnaeus) is the most common organism on the upper and lower shore. The mid-intertidal zone is dominated by the alga *Ascophyllum nodosum* (Linnaeus) LeJolis, *Mytilus edulis* Linnaeus and *Chondrus crispus* Stackhouse. Each accounts for less than 10% of the cover in the low intertidal zone. The second site is about 1.0 km west of the Long Cove site on the southern edge of Mill Pond Point. This site is a semiprotected boulder beach but shows similar composition of species and zonation to the Long Cove site. The exception is *M. edulis* which is more common and accounts for 57% of the cover at Mill Pond Point.

Radular activity of *Littorina* species was recorded with a portable cassette tape recorder (Radio Shack Realistic, CTR 48, Model 14-802) and an underwater microphone. All recordings of snails were done without removing the snails and on smooth, bare surfaces unless otherwise noted. The microphone was held 2-3 cm from each periwinkle. Because a snail would usually stop grazing when first approached, a recording was started when a snail resumed grazing and continued for about 20 rasps. Each recording was timed with a stopwatch, and the data were converted to rasps/min.

From 10 June to 2 August 1982, 121 successful recordings were made of individuals of the genus *Littorina*

Table 1

Means and standard deviations for 1982 recordings. Locations (LC for Long Cove, MP for Mill Pond) and dates (month/day) of sampling are grouped by intertidal position and are for Low: LC-6/11, MP-6/15; for Mid: LC-7/27, LC-8/4; for High: LC-6/10, MP-7/28, LC-8/2. Sample sizes are given in parentheses. Snails were recorded on either bare rock, *Semibalanus balanoides*, or *Ascophyllum nodosum*.

Intertidal position	<i>L. littorea</i>			<i>L. saxatilis</i>	<i>L. obtusata</i>
	Bare rock	<i>S. balanoides</i>	<i>A. nodosum</i>	Bare rock	<i>A. nodosum</i>
Low	30.6 ± 5.8 (13)	22.2 ± 3.9 (8)	—	—	—
Mid	31.0 ± 3.4 (8)	25.0 ± 4.0 (2)	33.0 ± 7.1 (22)	—	35.6 ± 7.2 (17)
High	34.8 ± 5.1 (29)	—	19.9 (1)	37.4 ± 4.2 (9)	41.8 ± 10.3 (12)

(83 of *L. littorea*, 29 of *L. obtusata* and 9 of *L. saxatilis*). The position of each snail in the intertidal zone was noted. Most observations were made on the incoming tide and on snails that had been covered for less than 30 min. Although data were collected under a variety of conditions, four comparisons were planned: among samples for *L. littorea* on bare surfaces, between *L. littorea* and *L. saxatilis*, between *L. littorea* on rock and *L. obtusata* on *Ascophyllum nodosum*, and for *L. littorea* on bare versus barnacle-covered rock. For all tests, Bartlett's test for homogeneity of variances was not significant, and data were analyzed by analysis of variance (SOKAL & ROHLF, 1981).

In 1983 only individuals of *Littorina littorea* were recorded and all 157 recordings were done in June. No snail was recorded more than once. The position of each snail relative to fixed markers on the shore was noted. The shore was divided by the markers into three roughly equal zones (low: less than 0.7 m above MLW; mid: 0.7 to 1.6 m above MLW; high: more than 1.6 m above MLW). After each recording, the height of the snail's shell was measured to the nearest millimeter. We also noted whether the snails had just been covered by the tide (less than 5 min) or covered for more than 30 min. The category of more than 30 min includes some animals that were re-

corded on the outgoing tide. Kruskal-Wallis tests were used to examine differences in radular activity because variances were not homogeneous. A regression of activity on length of snail was also done.

The radular activity of *Littorina littorea* on *Semibalanus balanoides* and on bare surfaces was also compared. Snails were removed from the lower shore and placed on a submerged rock that was either bare or covered with *S. balanoides*. The rasping rate of each snail was recorded on both types of surfaces, and the order of presentation of surfaces to each snail was random. Pairs of recordings were successfully obtained for 19 snails during 16 to 18 June 1982 and 16 snails during 20 to 28 July 1983. Because periwinkles were only intermittently active on *S. balanoides*, it was impossible to get good sequences of 20 rasps. Data were therefore tallied as the number of rasps in the first 30 sec after the first rasp, and analyzed as a paired *t*-test (SOKAL & ROHLF, 1981).

RESULTS

Observations of radular activity in 1982 are summarized in Table 1. The rate of radular activity of *Littorina littorea* on bare surfaces varied with date and location of sampling

Table 2

Summary statistics for 1983 recordings. Means and standard deviations are given for rasps/min, for lengths of snails that were recorded, and for residuals from overall regression. Snails were recorded within 5 min of submersion (<5) or after 30 min of submersion (>30).

Intertidal position	Time	Sample size	Rasps per min	Length	Residual
Low	<5	31	34.1 ± 11.0	10.4 ± 3.6	-2.96 ± 10.56
	>30	25	35.7 ± 6.8	11.4 ± 3.5	-0.84 ± 6.78
Mid	<5	30	33.5 ± 5.8	10.7 ± 3.2	-3.38 ± 5.00
	>30	12	40.5 ± 9.8	10.5 ± 2.6	+3.53 ± 8.94
High	<5	32	40.6 ± 5.7	12.2 ± 3.7	+4.48 ± 5.35
	>30	27	37.0 ± 4.9	12.6 ± 3.6	+1.06 ± 5.26

($F = 3.00$, with 5 and 44 d.f., error mean square = 23.6). Significant treatment effect was caused by one sample from Mill Pond that had a much lower mean (27.6 rasps/min), and all unplanned comparisons among samples were not significant. We cannot reject the null hypothesis of no difference for snails from different intertidal zones, for snails from Long Cove versus Mill Pond, and for snails from early (June) versus late (July and August) summer. Both *L. obtusata* and *L. saxatilis* showed rates of radular activity similar to *L. littorea*. Only when found on barnacle-covered rocks, did *L. littorea* graze more slowly ($F = 16.73$, with 1 and 29 d.f., error mean square = 21.2).

For the data collected in 1983, radular activity of *Littorina littorea* was higher for animals from the high intertidal zone (Table 2). The Kruskal-Wallis test was significant ($T = 9.74$, d.f. = 2); however, the effect could have been due to variation of activity with the size of the animal because the high intertidal snails were also larger. The regression of activity on length was significant ($F = 8.40$, with 1 and 155 d.f., residual mean square = 58.83), and shows that larger animals graze more slowly. The model is rasps/min = $42.4 - 0.5(\text{length})$. To correct for effects of body size, the Kruskal-Wallis test among low-, mid- and high-zone snails was re-done using the residuals from the regression. There remained a significant difference ($T = 14.73$).

No difference in activity was detected for animals just covered by the tide versus those covered for more than 30 min (Table 2). Kruskal-Wallis tests were not significant for either the raw data ($T = 0.08$) or the residuals from the regression ($T = 0.05$).

In the paired comparison experiment, periwinkles showed about a 30% decline in the number of rasps when placed on a barnacle-covered surface. The overall mean rate on *Semibalanus balanoides* was 10.2 rasps/30 sec (SD = 4.44) while on bare surfaces the rate was 13.9 rasps/30 sec (SD = 3.86). For pairs of observations of the same snail on both surfaces, the mean difference was 4.0 rasps/30 sec (SD = 5.21), and the paired *t*-test is significant ($t = 4.54$, $n = 35$).

Our observations suggest that periwinkles have difficulty when grazing among barnacles. A snail frequently stopped moving its radula. During these stops, a snail would move its head from side-to-side, and it appeared that the snail was searching for a better surface upon which to graze. Continuous activity on barnacles occurred only on smaller *Semibalanus balanoides* and in small open patches among the barnacles.

DISCUSSION

NEWELL *et al.* (1971) showed that *Littorina littorea* from upper intertidal shores had a higher feeding rate than those from lower shores. Our results are not as striking. Although snails from the high intertidal do graze at a faster rate, the difference is not large. The percent differ-

ence is 16% ($[(40.6 - 34.6)/40.6]$; data from Table 2). We thus infer from our data that the individual impact of *L. littorea* should be greater in areas that are submerged for longer periods even though there is some compensation of radular activity. Although this is consistent with observed damage to algae (LUBCHENCO, 1978, 1982, 1983; LUBCHENCO & MENGE, 1978; MENGE, 1976), both NEWELL *et al.* (1971) and our results are based on the assumption that rates of activity are constant, or at least vary in a similar fashion, over the tidal cycle. Confirmation requires *in situ* measurements throughout the tidal cycle.

NEWELL *et al.* (1971) reported maximal feeding rates of 16 to 36 rasps/min for animals from low to high intertidal levels (fig. 5 in NEWELL *et al.*, 1971), and much lower average rates than ours (6.1 to 28.4 rasps/min from table 3 in NEWELL *et al.*, 1971). We found, however, average rates of 33.9 to 38.8 rasps/min (Table 2). It is possible that the lower rates found by NEWELL *et al.* were due to handling the snails. When we recorded radular activity of snails that had been handled, we found a mean rate of 23.6 rasps/min (SD = 3.68, unpublished data). This rate is similar to rates observed by NEWELL *et al.* (1971) and when compared to our *in situ* measurements, which ranged from 27.6 ± 2.0 (one sample from Mill Pond) to 38.8 ± 6.2 (Table 2), is quite low.

We did not find any variation in radular activity at different times during the tidal cycle as reported by NEWELL *et al.* (1971). This is consistent with results for patellid limpets (BOYDEN & ZELDIS, 1979). A good predictor of activity is body size and even this explains only 5% of the variation observed in the data.

Our direct measurements of radular activity on barnacle-covered surfaces and bare rocks are quite consistent across experiments. *In situ* measurements show a 31% decline in activity on *Semibalanus balanoides*; this is an average reduction of 10.3 rasps/min (Table 1). Paired observations of the individual on bare versus *Semibalanus*-covered rocks show a 27% reduction or about 8 rasps/min. Assuming that each movement of the radula clears the same amount of material, the refuge from grazing that is provided by crevices is substantial. We consider this 30% reduction a minimum estimate because rasps by *Littorina littorea* on *S. balanoides* tend to be shorter in duration, and we suspect less material may be taken per rasp.

On *Ascophyllum nodosum*, *Littorina obtusata* shows a similar rate of radular movement to *L. littorea* on bare rock (Table 1). *Littorina obtusata* is commonly found on submerged plants of *A. nodosum* at both of our sites. Recordings indicate that *L. obtusata* is grazing on *A. nodosum*, and inspection of plants shows that *A. nodosum* is damaged by grazing activity. On bare surfaces, *L. saxatilis* appears to graze at slightly higher rates than *L. littorea*, although the difference is not significant (Table 1).

Although we found a large amount of variation among individuals in the rate of radular movement, it is clear

that surface conditions have a far greater effect than body size or intertidal position on the rate of rasping. Comparison of individuals on the high shore with those on the low shore shows only a 4–16% decline in activity (Tables 1, 2). Body size has a similar effect; our regression model predicts a 15% decline in activity when the smallest (6 mm) and the largest snails (17 mm) are compared. Compared to these data, the 30% decline we observed when *Littorina littorea* grazes on barnacle-encrusted surfaces is quite striking. Given the amount of variation we have seen among individual snails, it is possible that subtle differences in surface conditions and their effect on effectiveness of *L. littorea* grazing may be as important as changes in density of grazers.

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